

Vol. 25. Parts 7-9. Pp. 67-98, 24 figs., 1 plate. 15th Sept., 1950

THE PROCEEDINGS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Series A

GENERAL ENTOMOLOGY

World List abbreviation : *Proc. R. ent. Soc. Lond.* (A)

CONTENTS

	PAGE
HICKIN, N. E., Ph.D., F.R.E.S. Larvae of the British Trichoptera : 28	67-70, 12 figs.
HICKIN, N. E., Ph.D., F.R.E.S. Larvae of the British Trichoptera : 29	71-74, 8 figs.
VESEY-FITZGERALD, DESMOND, B.Sc., F.R.E.S. Nesting habits of some aculeate Hymenoptera in the Seychelles	75-80, 1 plate.
VESEY-FITZGERALD, D., B.Sc., F.R.E.S. Notes on the Genus <i>Ropalidia</i> (Hymenoptera : VESPIDAE) from Madagascar	81-86
RAINEY, R. C., Ph.D., A.R.C.S., F.R.E.S. The embryonic respiration of the Sheep Blowfly, <i>Lucilia sericata</i> Mg. (Diptera: CALLIPHORIDAE)	87-92, 2 figs.
THOMAS, H. T., Field notes on the mating habits of <i>Sarcophaga</i> Meigen (Diptera)	93-98, 2 fig.
BOOK NOTICES	86

LONDON

PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 12s. 0d.

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LARVAE OF THE BRITISH TRICHOPTERA: 28.

By N. E. HICKIN, Ph.D., F.R.E.S.

Tinodes waeneri L. (PSYCHOMYIDAE).

THIS widely distributed caddis inhabits ponds, lakes and slow rivers. It is particularly abundant in Lake Windermere, where the larvae may be found in considerable numbers in their mud tunnels on large stones or rocks, usually 6 ft. or so from the edge of the lake. In July and August the adult flies are fond of sitting on oak leaves in those situations where oaks grow near the water's edge, as on Windermere. It should be mentioned that the other seven British species of the genus *Tinodes* are uncommon, local or rare, but *T. waeneri* is the largest.

I am indebted to Dr. T. T. Macan, Mr. G. Thompson and Mr. S. Nield, of the Freshwater Biological Association for getting live *T. waeneri* larvae from Wray Castle, Windermere, to my home in Surrey during a hot midsummer.

Larva (fig. 1).—Campodeiform, head procentrous, legs small in relation to size of body, larva uniformly cylindrical. When seen from above, the head, prothorax and last abdominal segment less wide than the rest of the body, and a slight tapering from about the fourth abdominal segment is evident when the larva is moving.

Length 10 mm. Width 1.2 mm.

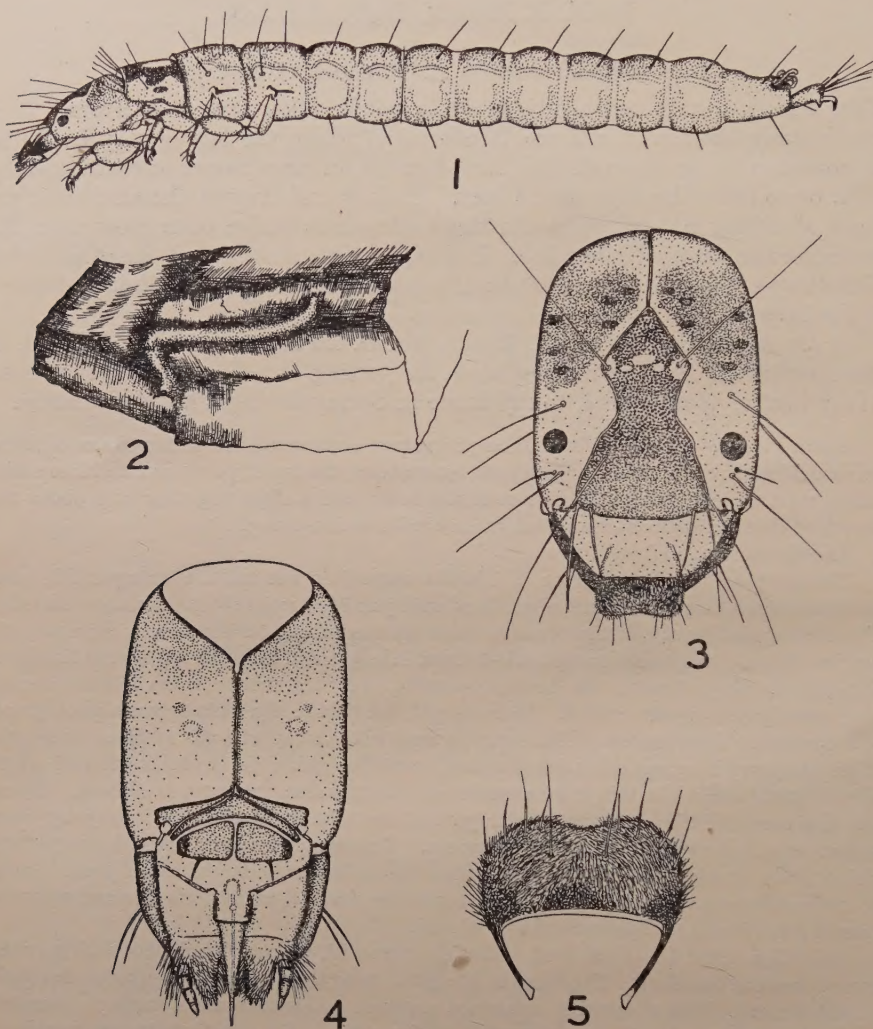
Larval tunnel (fig. 2).—Larvae of *Tinodes waeneri* do not make a transportable case, but construct a long thin tunnel of mud and sand particles, vegetable debris, algae and silk. The large quantity of silk that goes to make up the tube gives the tube a characteristic greyish colour. The tubes are up to 30–35 mm. in length and from 1.5–2.0 mm. in diameter. Superficially they resemble the tunnels constructed by the marine worm *Pomatoceros*, as they are often sinuously curved. Wesenberg-Lund (1943: fig. 156B) gives a photograph of a number of these tunnels. The tunnel is fixed to the stone with silk all along its length. When the larva is approaching full growth the anterior end of the tunnel is widened (up to about 6 mm.) and it is in this wider anterior end that the change to pupa is effected. When this has occurred the narrow posterior part of the tube is often washed away by wave action (as on Lake Windermere) or by currents. The larva spins extra silk before pupation, which fairly closely envelops the pupa when the metamorphosis has taken place. It is, however, adherent to the inner wall of the tunnel, so that it does not form a cocoon separate from it (cf. *Tinodes pallidula* and *Lype reducta*).

Head (figs. 3 and 4).—Oval, long, yellowish or greenish-yellow with clypeus dark greyish-brown, oral end less dark. The areas of the genae near the vertex of the clypeus also dark greyish-brown. Eyes situated in a forward position. Antennae small, bulbous, situated in pit-like foldings of the anterior margin of the genae. The mouthparts are capable of considerable extension; both figures of the head show the mouthparts in the extended position.

Labrum (fig. 5).—Sclerotised, dark brown, darkest at lateral areas of the hind margin, prolongations of hind margin long and black in colour except distal tips. Anterior marginal excision shallow and wide. The whole labrum is covered with fine hairs.

Mandibles.—Asymmetrical, scoop-shaped. Teeth sharper on left mandible, auxiliary toothed area at base of each mandible on inner edge and outer teeth of the opposite mandibles grind against them (only one pair at a time, of course). Each mandible has two bristles on the outer edge, but only the left mandible has a brush of hairs on the inner edge.

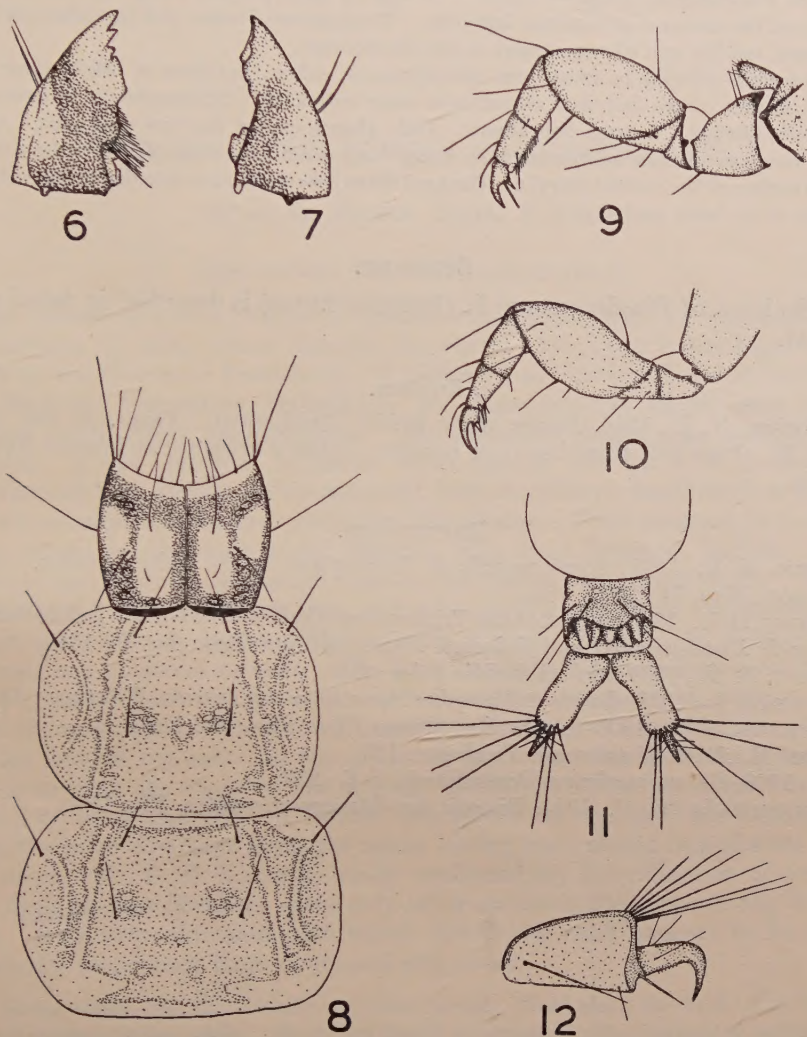
Maxillae.—Maxillary palp four-segmented, the third segment being the longest; mala covered with hairs directed inwards, the inner hairs turning outwards as they meet the long acicular *labium*. Base of labium with sclerotized collar-like ring. Labial palps absent, but a pair of fine hairs present on ventral surface.



FIGS. 1-5.—*Tinodes waeneri* L.—(1) Lateral view of larva. (2) Larval tunnel. (3) Head from above. (4) Head from below. (5) Labrum.

Gular sclerite does not divide the genae, it is bow-shaped; lying just anterior to it is a pair of large sclerites. In the genae just posterior to the gular sclerite is a black, thickened furrow, which, commencing from the oral extremity of the ventral genal suture, is directed outwards until it reaches a point opposite the outer horns of the gular sclerite when it curves forwards to finish on a cube-shaped organ immediately adjacent to the outer horns of the gular sclerite.

Thorax.—Only the prothorax sclerotised. Prosternal horn absent. Prothorax only slightly wider than the head, very dark brown except for four large creamy-yellow areas, the median pair being larger. Anterior margin also creamy yellow. Ventral posterior margin black and produced forwards in the median line to form a robust spine-like projection. Meso- and metathorax larger than prothorax, dorsal surface light chestnut



FIGS. 6-12.—*Tinodes waeneri* L.—(6) Left mandible. (7) Right mandible. (8) Thoracic nota. (9) Prothoracic leg. (10) Mesothoracic leg. (11) Anal segments from above. (12) Anal claw from the side.

brown with greenish-mauve tinge, which is given by presence of minute spicules, with very variable pattern of white streaks and spots (when the spicules are absent); pleural and ventral regions bright apple green. The amount of green coloration is subject to wide variation. Some larvae are vivid bluish-green, whilst other larvae are found with the green colour entirely absent.

Legs.—Small in relation to size of body. Prothoracic legs slightly larger than meso- and metathoracic legs. Tarsal claws capable of considerable flexion in relation to tarsus when tarsal spines interlock with tarsal claw. On all tarsal claws a bristle is present on the claw in addition to the spine at the base. A flap-like forward extension of the trochantin is present which bears a few hairs. (This is present also in POLYCENTROPIDAE, such as *Plectrocnemia conspersa* Curtis.) Fringe of hairs present along the entire hind margin of the tarsus of prothoracic legs only. Trochantins of meso- and metathoracic legs are black, rod-like and stirrup-shaped at the anterior end.

Abdomen.—Similar to meso- and metathorax in colour, but area of bright green on dorsal surface of the last four segments is more extensive. Intersegmental grooves of abdomen distinct. Lateral line absent. Gills absent except for five anal gills. Anal claws borne on distinct cylindrical lobes which bear seven long stout black bristles on the upper surface of the ventral margin. The anal claws bear six minute spicules on the ventral margin of the basal part.

SUMMARY.

The larva of *Tinodes waeneri* L. (PSYCHOMYIDAE) is described in detail and figured.

Erratum.

Hickin, N. E., 1946, *Larvae of the British Trichoptera*. *Trans. R. ent. Soc. Lond.* **97**. Page 202, third line from bottom: delete *Phryganea* and insert *Hydropsyche*.

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 WESENBERG-LUND., C., 1943, *Biologie der Süsswasserinsekten*, Fig. 156B.

LARVAE OF THE BRITISH TRICHOPTERA: 29.

By N. E. HICKIN, Ph.D., F.R.E.S.

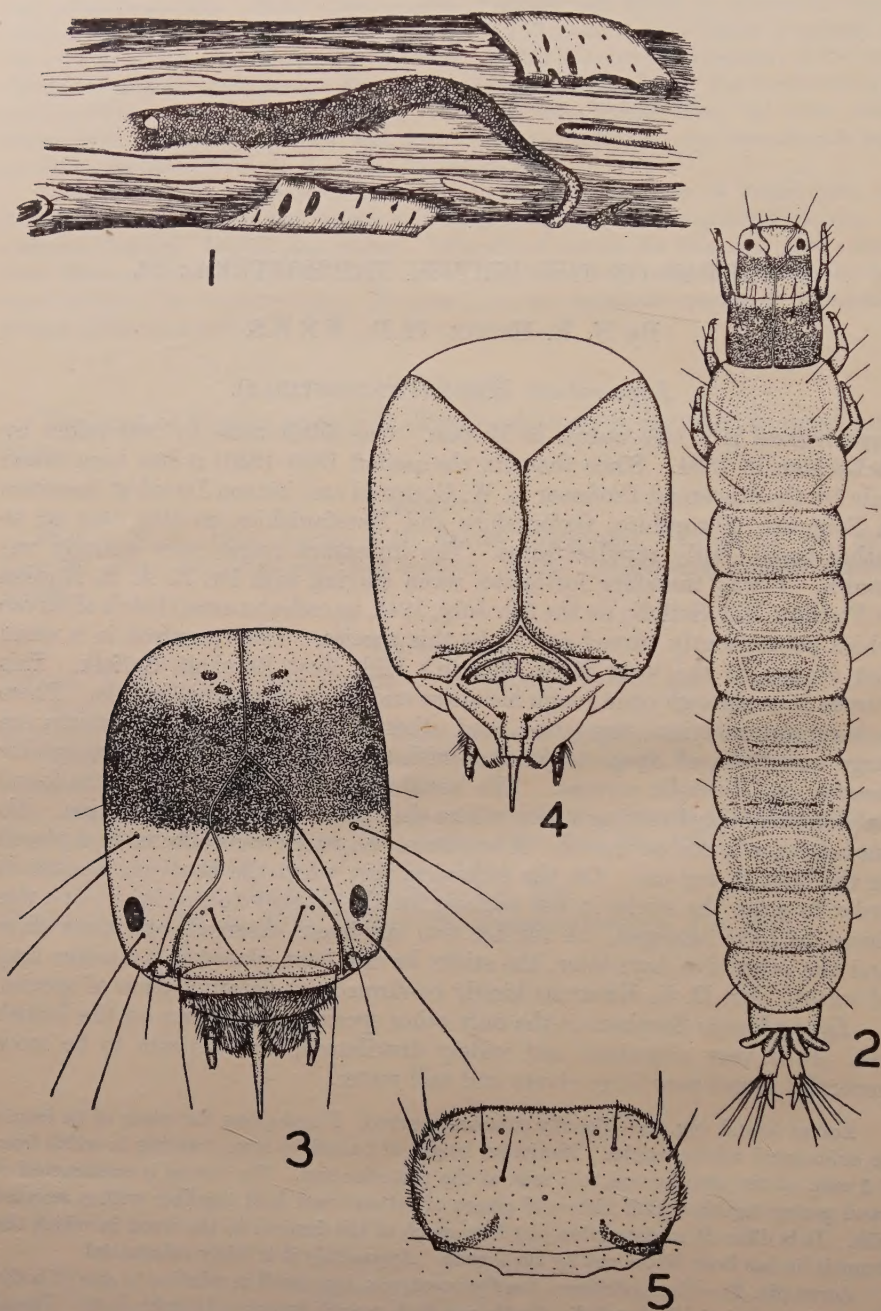
Lype reducta Hagen (PSYCHOMYIDAE).

Lype reducta is a rare caddis in Britain. One adult male fly was taken by McLachlan in 1884. Since then (in the period 1936-1940) it has been taken only by the Reverend Professor L. W. Grensted and his son David at localities in Somerset, Shropshire, Oxfordshire and Herefordshire, mostly near or at rather small, fairly rapid streams. The immature stages were entirely unknown. I was therefore fortunate, when staying with Dr. E. A. R. Ennion at Flatford Mill, Suffolk, on the 5th July, 1949, to collect a small batch of larvae which subsequently turned out to be this species. They occurred in a small fast stream to the west of St. Martin's Hill, East Bergholt, Suffolk. This stream runs through open rough meadows and skirts some small woods. There is luxuriant marginal vegetation, and other caddis present in the stream are large quantities of *Agapetus fuscipes* with a smaller number of *Limnophilus lunatus* and *Anabolia nervosa*. The larval tunnels of *Lype reducta* were found only on submerged rotting sticks, where the stream ran alongside a copse. No tunnels were found on stones. A bundle of the sticks was collected and placed in the boot of my car. On the following day, when the boot was opened in order to wrap the sticks in wet sacking for the journey to my home, one was found to have emerged. A further two specimens emerged, one three days and the other five days later, the sticks having been placed in a shallow tray of water. Mr. D. E. Kimmins kindly confirmed my determination of species.

Lype phaeopa Stephens is the only other species in the genus on the British list. It is very abundant and widely distributed, and appears to be more generally found near large rivers and still water.

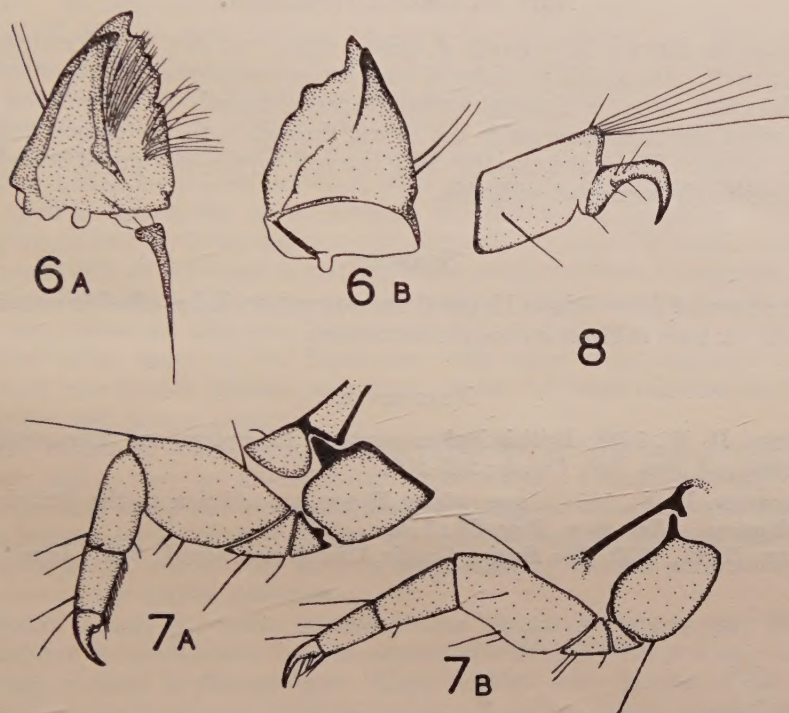
Larval tunnel, (fig. 1).—Usually sinuously curved. Fixed along the whole of its length to submerged rotting sticks. Maximum length of tunnel 75 mm., varying in width from 5.5 mm. at the anterior end to 1 mm. at the posterior end. The tunnel is constructed of sand grains together with bitten-off pieces of rotten wood held together with a secreted silk. It is difficult to determine just how much of the furrows in the wood in which the tunnels lie has been bitten out by the larvae. Apparently it is fairly substantial.

Larva (fig. 2).—Campodeiform, head procntrous, legs small in relation to size of body. Head characteristically banded. Prothorax dark greyish-brown with light spots. Dorsal surface of rest of body pinkish with mauve sheen shading to cream laterally and underneath. Length 11 mm.; width 1.5 mm. Head, thorax and last two abdominal segments not as wide as the rest of the body. All the mouthparts are capable of complete retraction



FIGS. 1-5.—*Lype reducta* Hagen.—(1) Larval tunnel. (2) Larva from above. (3) Head from above. (4) Head from below. (5) Labrum.

into the head capsule. *Head*.—Oval, oral half light yellow, aboral half dark brown, shading to light yellow aborally. The vertex of the clypeus is included in the dark area. Eyes situated forwards, antennae small. *Labrum*.—Strongly curved, so that seen from above the ventral rods appear covered by the labrum. Excision on anterior margin shallow. Anterior half covered with fine hairs. *Mandibles* (figs. 6a and 6b).—Asymmetrical, blunt and scoop-shaped. Five teeth on left mandible, four on right. Two bristles on outer edge of each mandible, but brush of long hairs on inner face of left mandible only. These hairs arise from two distinct areas. Right mandible somewhat thicker than the left. *Maxillae* (figs. 3 and 4).—Palps four-segmented, third segment longest, mala hairy, the hairs being directed inwards. *Labium*.—Long and acicular, labial palps absent but bearing pair of fine hairs on ventral surface. Base of labium consists of ring-like collar supported by sclerotized rods.



FIGS. 6-8.—*Lype reducta* Hagen.—(6a) Left mandible. (6b) Right mandible. (7a) Prothoracic leg. (7b) Mesothoracic leg. (8) Anal claw.

Gular sclerite.—Genae not divided by the gular sclerite. Genal suture sinuous. Gular sclerite shaped as in fig. 4, with lateral horns directed outwards and forwards. The paired sclerites lying anterior to the gular sclerite less deep than in *Tinodes waeneri*. *Thorax*.—Only prothorax sclerotized. Prosternal horn absent. Prothorax only slightly wider than the head, dark greyish brown with four light creamish-yellow spots, inner pair anterior to outer pair and a long bristle arises from centre of each. Anterior margin creamish in colour, posterior margin black. Meso- and metathorax wider than prothorax, pinkish in colour with mauve sheen, light cream laterally and underneath. The pinkish colour of the dorsal surface appears to be given by minute spicules, which are absent from a pattern of light streaks and spots, which, however, is very variable. *Legs*.—Relatively small for

size of larva. All legs approximately equal in length, but prothoracic legs slightly larger and more robust than meso- and metathoracic legs. Tarsus of prothoracic legs only with fringe of small hairs along entire hind edge. A large peg on the anterior margin of the coxa articulates with the trochantin. Large flap-like anterior extension of the trochantin present. Tarsal claws of all legs bear a bristle in addition to a spine at the base. Both spines and bristles are, however, often lost on the prothoracic claws. *Abdomen*.—Lateral line absent. Width of segments, coloration and pattern of light streaks and spots similar to meso- and metathorax, but very variable. Eighth segment triangular, ninth segment small and cylindrical, bearing five anal gills. Anal claws simple. I have not been able to find the series of six minute spicules on the ventral margin of the basal part of the claw, as found in *Tinodes waeneri* L.

NOTE ON COCOON FORMATION.

When the larva is fully grown it spins a silken web-like cylindrical cocoon around itself. On to this particles of sand become somewhat loosely attached, but the whole cocoon is situated within the larval tunnel—at the anterior end. Thus when the pupa emerges it has to cut through both the cocoon and the larval tunnel. The exceptionally long curved scythe-like pupal mandibles may be directly connected with this.

SUMMARY.

The larva of *Lype reducta* Hagen (PSYCHOMYIDAE) is described in detail and figured. A note is given on cocoon formation.

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McLACHLAN, R. F., 1884, *Lype reducta* Hagen, an addition to the British Trichoptera. *Ent. mon. Mag.* 21 : 113.
MOSELY, M. E., 1939, *The British Caddis Flies (Trichoptera)* : 224. London.

NESTING HABITS OF SOME ACULEATE HYMENOPTERA IN THE SEYCHELLES.

By DESMOND VESEY-FITZGERALD, B.Sc., F.R.E.S.

It is not surprising that islands so remote as the Seychelles are extremely poor in species of Aculeate Hymenoptera. However, individuals are often abundant, and so observation of their habits is easy. Meade-Waldo and Turner have given lists of the species collected by members of the Percy Sladen Expedition early in the present century, and Bequaert noted the curious coloration shared by three, probably the only three, really endemic wasps, namely, *Eumenes alluaudi* Perez, *Odynerus seychellensis* Dalla-Torre and *Crabro scotti* Turner. In this connection it is interesting to note that the same author records *E. alluaudi* from Glorioso Island in the Mozambique Channel, adding that, "very likely it is to be found also in the Comoros." If he implies by this statement that the wasp is indigenous to those islands it is the opinion of the present author that this is most unlikely. The *Eumenes* found on the small southern islands near the coast of Madagascar is *E. marillosus* (Degeer), specimens of which have been collected both on Astove and Cosmoledo Islands. The periodic appearance of *E. alluaudi* on Glorioso, or any other island in shipping contact with Seychelles, could easily be explained by wasps emerging from mud cells on furniture or packing cases, which had been transported from its original locality. The same remarks apply to *Odynerus seychellensis*, which has been taken on Alphonse Island, which is a sand cay lying some three hundred miles south of the Seychelles. The more usual *Odynerus* of the southern islands is *O. farquharensis* Cam., which has been collected on North Farquhar and Astove Islands.

The remaining wasps recorded from Seychelles all have ranges outside the islands, and so they are probably introduced forms. *Trypoxylon saitifrons* de Saussure and *Sceliphron violaceum* Dahlbom are, for example, common, and therefore not easily overlooked, but are recorded here for the first time from the archipelago, and so they have in all probability become established since the days of the earlier collectors.

Small though the fauna is, and diverse though its origins may be, the majority of the species have become associated with each other in a very curious although entirely haphazard way. Huge boulders are a feature of the landscape of the Seychelles and under the ledges of these, or in deep recesses between adjacent rocks, caverns of various sizes often occur.

Such places provide ideal shelter for Mason wasps because if their cells were exposed to the heavy rain of the Seychelles, they would have little chance of survival. For this reason apparently the walls and ceilings of these caverns become plastered with hundreds of thousands of cells made by many generations of wasps. Subsequently the empty cells of the Mason wasps provide attractive nesting sites to a variety of other species of Hymenoptera which do not construct their own nests. In this way many species are brought together which, though they can and do nest separately, are so often found together in the Seychelles that a sort of loose community is built up.

The first member of this assemblage to be studied was *Eumenes alluaudi*. This wasp is common on Mahé and Praslin Islands and in certain localities many

thousands of old cells may be seen on sheltered rock walls. Sometimes these conglomerations are entirely composed of this species, but more frequently the cells of the *Eumenes* are mixed with those of *Sceliphron hemipterum* Fabricius. The *Eumenes* also constructs its cells elsewhere on house walls and on furniture.

The foundation of the cells of *Eumenes* is laid by constructing a ring of mud on a flat surface, that is to say the cell is not floored with mud, but the supporting surface is exposed on the inside as part of the wall of the chamber. Upon one occasion the building work of this wasp was watched in detail.

When observations started the "pot" was already half finished and the further progress of bringing mud, setting it in place and departing for more was as follows :

Time.						
Arrivals.				Departures.		
Hr.	Mins.	Secs.		Hr.	Mins.	Secs.
—	—	—	.	11	53	—
11	54	30	.	11	56	30
11	58	—	.	11	59	30
12	0	30	.	12	2	—
12	7	—	.	(Did not settle)		
12	8	—	.	12	10	—
12	11	30	.	12	13	—
12	18	30	.	12	20	—
12	21	30	.	(Departed without settling)		
12	23	—	.	12	24	—
12	25	—	.	12	26	30
12	32	—	.	12	34	—
12	35	30	.	12	36	30
12	38	30	.	12	40	—
12	41	30	.	12	43	—
12	48	30	.	(Departed almost at once)		
12	51	30	.	12	52	30
12	55	—	.	12	56	30
12	58	—	.	12	59	—

At this juncture the pitcher was complete, and so if the same rather feverish and sustained activity had been maintained from the beginning the finished work must have taken about two hours in all. The "neck" of the "pitcher" was now commenced and the fashioning of this part was carried out more slowly and carefully.

The wasp arrived again with a load of mud at 13.00 hours and worked for two minutes. She then departed and fetched another load, arriving at 13.04 hours, worked for three minutes, departed and returned with her last load at 13.08 hours. She then worked away, shaping the flange of the neck for seven minutes, all the time going round and round and inspecting the work with her antennae until everything was smoothed off to her satisfaction. At 13.15 hours she climbed on top of the pitcher and inserted the tip of her abdomen through the neck to oviposit. At 13.17 hours she flew away and the glistening white egg could be seen adhering to the top of the cell.

The egg is suspended from the roof of the chamber and it hatches in about three days. As soon as the egg is laid the wasp sets about storing the cell with caterpillars. The time taken to store the cell must vary upon the fortunes of the hunter, but it is usual for the cell to remain open several days and hence storing may be continued after the young wasp larva has hatched from the egg. When the store is complete the wasp demolishes the neck of the cell and seals the entrance. It is rare for the neck not to be demolished. Immediately the last cell is closed the foundations of a new cell are laid adjacent to the former one. The wasp never spends the night on or near the cells even while work on them is in progress.

When fully-fed the larva spins a cocoon which is tissue paper-like and is partly free and partly adhering to the cell wall. The wasp is ready to emerge about three weeks after the date upon which the egg was laid; the larva seems to feed for about one week, so the pupal period probably lasts for rather less than a fortnight. The wasp is completely ready for flight before it leaves the cell through the mud wall of which it bites with its mandibles. If the young wasp is a female, males are attracted to the cell in numbers immediately before the young wasp is ready to emerge. So quick, however, is the exit of the wasp when once a hole has been bitten through the cell wall that often the female eludes the vigilance of the waiting males.

Eumenes larvae are frequently parasitized by a Chalcid wasp, but the species has not yet been determined.

Sceliphron hemipterum is the second common wasp to share the rock shelters as a nesting site. Like the *Eumenes* the present species is only incidentally gregarious and it often constructs its mud cells elsewhere on house walls and furniture. In order to throw some light on the biology of this species two females were watched over a period of time and their daily work recorded. The result of these observations appear to be of sufficient interest to be given *in extenso*.

Wasp No. 1 was observed at Mamelle Estate, Mahé, on 28.vii.38. When the observations commenced one cell was already complete and this cell was superimposed on a block of three old cells which, however, were not the work of the present female. During the first day two spiders were stored in the cell and an egg was laid on the abdomen of the innermost. At dusk the mouth of the cell was sealed. At night the female never rested anywhere in the vicinity of her cells.

29.viii: Cell reopened and storing of spiders continued. During the day the store was completed and the cell finally sealed. Cell No. 2 was then built and completed by evening and left open and empty during the night.

30.viii: Storing of cell No. 2 in progress, but by evening only one spider had been caught. An egg had, however, been laid on the abdomen of the spider, and in the evening the cell was sealed for the night.

31.viii: Cell No. 2 reopened and storing completed and the cell finally sealed in the evening.

1.ix: Cell No. 3 was built and completed; no storing took place, but cells No. 1 and 2 were replastered with mud. Cell No. 3 was left open and empty for the night.

2.ix: Storing of cell No. 3 was commenced, but not completed; an egg was laid and the cell was sealed for the night.

3.ix: Cell No. 3 was reopened, storing completed and the cell finally closed.

Cell No. 4 built; one spider stored; egg laid on abdomen and cell closed for the night.

4.ix: Cell No. 4 reopened, storing completed and finally closed.

5.ix: Cell No. 5 built and closed for evening, but contents not observed.

6.ix: Cell No. 5 reopened and closed for evening, contents again not observed.

7.ix: Cell No. 5 reopened and seemed to be half full of spiders, storing completed and finally closed.

8.ix: Cell No. 6 was built and closed for the night, but contents not observed.

9.ix: Cell No. 6 reopened and closed for the night, but contents not observed.

At this juncture no more observations were possible until 17.ix, by which date several new cells had been made, but it was impossible to count them, as the whole mass had been plastered over with mud. The wasp was, however, still working on a partially stored open cell, which may for convenience be referred to as cell "No. a." This cell was closed for the night.

18.ix: Cell No. a reopened, storing continued and closed for the night.

19.ix: Cell No. a reopened (it was half full), storing completed and cell finally closed.

20.ix: Cell No. b built and left open and empty for the night.

22.ix: Cell No. c was then built and left open and empty for the night.

23.ix: Only one spider was stored upon the abdomen of which an egg was laid. Cell No. c was then closed for the night.

24.ix: Cell No. c reopened, storing continued and cell closed for the night.

25.ix: Cell No. c reopened, storing completed and cell finally closed.

26.ix: Cell No. d built and left open and empty for the night.

27.ix: Cell No. d partially stored and closed for the night.

28.ix: Cell No. d reopened, storing completed and cell finally closed.

29.ix: Whole mass of the cells plastered over.

30.ix: Cell No. e built and left open and empty for the night.

1.x: No work.

2.x: Whole mass of cells plastered over, but cell No. e remained open and empty.

3.x: Plastering continued. Cell No. e neglected.

4.x: No work.

5.x: No work.

6.x: Cell No. e, though empty, is closed, the whole nest is replastered and irregular ridges of mud are constructed over the mass of cells.

7.x: Ridge plastering continued.

8.x: Wasp pays frequent visits to nest, but no work done.

9.x: Same as yesterday.

10.x: Same as yesterday.

11.x: Cells No. 1, 2, 3, and 4 hatch out, and henceforth it is uncertain if the parent wasp again visited the nest. No observations were possible again until 29.x, during which time hatching continued.

Wasp No. 2 was also watched at Mamelle Estate, Mahé. When observations started on 17.i.39 four cells had been constructed, stored and closed, and cell No. 5 was complete and left open and empty for the night. Hereafter the record of operations was as follows:

18.ix: Storing of cell No. 5 commenced; closed for the night.

19.ix: Cell No. 5 reopened; storing continued until cell about half filled, then closed for the night.

20.ix: Cell No. 5 reopened, storing completed and cell finally sealed. The whole nest plastered over.

21.ix: Cell No. 6 was built and left open and empty for the night.

- 22.ix: Storing of cell No. 6 commenced; cell closed for the night.
 23.ix: Cell No. 6 reopened, storing completed and cell finally closed. Cell No. 7 built and left open and empty for the night.
 24.ix: Storing of cell No. 7 commenced; cell closed for the night.
 25.ix: Cell No. 7 reopened, storing completed and cell finally closed.
 26.ix: Cell No. 8 built, closed and plastered over.
 27.ix: Cell No. 9 built and left open and empty for the night.
 28.ix: Cell No. 9 closed.
 29.ix: No work.
 30.ix: Cell No. 9 reopened, but closed again for the night.
 1.x: Cell No. 10 built and closed for the night.
 2.x: Cell No. 10 reopened, but soon closed again. Cell No. 11 built and left open and empty for the night.
 3.x: Cell No. 11 closed.
 4.x: No work.
 5.x: No work.
 6.x: Nest plastered all over.
 7.x: Plastering continued. Daily observations interrupted for 17 days.
 24.x: By this date cells No. 1, 2 3 and 4 had hatched. The offspring are therefore ready to emerge—about five or six weeks after the parent finally closes the cell.

The remaining species of Hymenoptera belonging to the association all exploit the shelter provided by the empty cells of the *Eumenes* and *Sceliphron*. The most abundant of these is *Sceliphron violaceum*, which is always the commonest wasp about the mud-cell conglomerations, the males being especially conspicuous as they hang in clusters on any pendant root or straw which may be present. This wasp, moreover, has never been found nesting anywhere else in the Seychelles. The empty cell of either of the mason wasps is selected by this species and inside it stores spiders. The egg is laid across the abdomen of the prey, which is living but paralysed. When the larva is full-fed it spins a cocoon which is elongated, semitransparent, of a brown colour and very brittle. At the bottom of the cocoon there is a hard plug of excreta. After the excreta plug has been formed the full-fed larva rests as a prepupa for at least two days before pupating. The pupa is at first white. In five days the eyes become pigmented and in about three weeks after pupation the adult is ready to emerge.

S. violaceum is very frequently parasitized by an undetermined species of Chalcid. It seems probable that the present species is a particularly favoured host of this parasite, due to the fact that the old cells which it uses are often slightly cracked or that the new mud-plug with which it seals up the old exit hole of the former occupant does not fit very well.

Odynerus seychellensis is also a frequent tenant of the old *Eumenes* and *Sceliphron* "pots," but this wasp is also a frequent nester in other entirely unrelated sites, such as nail holes in buildings, etc.

Caterpillars are stored by this wasp. The fully-fed wasp larva lines the inside of its cell with a thin silken cover, giving the walls a glazed appearance. If the cell is very much too large for the *Odynerus* larva it partitions off a part of sufficient dimensions with a silken membrane. An excreta-plug is located plastered against the bottom of the space occupied by the pupa.

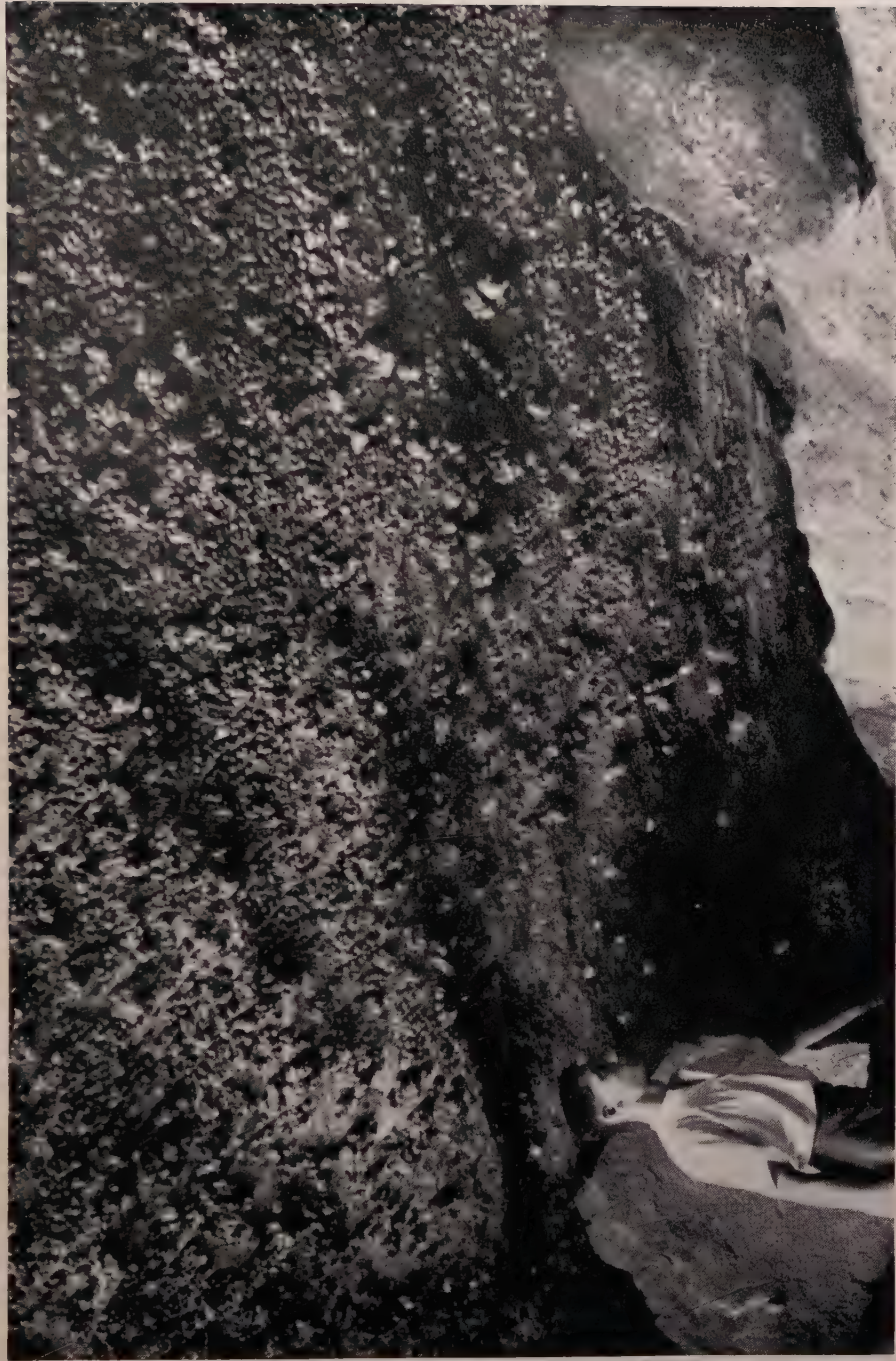
Two species of *Trypoxylon* are also frequently associated with the Mason wasp conglomerations. As with the other species the attraction is the nesting shelter provided by the disused cells. The species of *Trypoxylon* also nest elsewhere.

T. saitifrons stores its cells with small web-building spiders, eight of which completed the store in one cell examined. The larva feeds on this store, which is consumed in the course of one week. When full fed the larva spins a cocoon of a limp texture and transparent colour. While spinning the larva twists and turns within the limp bag in order to work from all angles. When completed the cocoon is stained a yellow colour. There is no excreta plug present. The brittle cocoon is supported in the cell by a peripheral web of floss. The young wasp is ready to emerge in from eighteen to twenty-one days.

T. errans de Saussure is a more abundant species. The prey of this species consists of small jumping spiders, which are stored in a semi-paralyzed state. Seven to nine complete the store. The wasp egg is laid on the abdomen of one. The larva feed for about one week, during which time every vestige of the stored prey is consumed. The full-fed larva rests a day or two and then starts to spin up. In three to five days the bottom end of the cocoon is filled with a hard plug of excreta. The end containing the excreta is swollen. The head end is held in position in the cell by a crown of floss. The young wasp is ready to emerge in just under three weeks. If an elongate cylindrical cavity is made use of as a nesting site the series of cells are divided from each other by a convex mud partition and the first formed is, of course, furthest inside. Under such circumstances it is evident that the oldest wasp must allow all the others to escape before it can itself get out. The times taken for individual development are variable, but there is no evidence that the rate of the development of the larva is adjusted to this need. In a series kept under observation the order of adult emergence was as follows: 2, 3, 6, 1, 5, 4.

Besides the wasps, bees also share the benefit of the ready-made shelter provided by the Mason wasps. *Megachile disjuncta* Fabricius makes free use of the cells of *Sceliphron*. The mud cell is heavily lined with a thick, wax-like substance which partially soaks into the mud walls. The bee's cell is then half filled with a wad of sticky, yellow pollen and upon the top of this is deposited the single white egg. The entrance to the cell is closed with a plug of the same wax and the outside of this is splashed over with mud, and at the same time part of the mud wall of the cell is splashed over with treacle-like wax. The larva rests in a curved position on top of the pollen store, which it consumes. When full-fed it spins a cocoon which is pale brown in colour, semi-transparent, flexible and paper-like in texture. The pupa is straight and rests with its head towards the entrance. A *Sceliphron* cell is large enough to shelter two of the bee's cells, and these are situated one above the other and divided from each other by a partition. The lower of the two invariably develops into a female and the upper into a male bee. The parent bee rests inside her cells during the night, a habit which the wasps never adopt.

The second species which has been found associated with the Mason wasp cells is *Megachile seychellensis* Cam. This species lines old *Sceliphron* cells with neatly cut, rectangular portions of leaf. Each of the bee's cells is composed of about fifteen portions, each bit bent round the bits within. Discs of leaf close the entrance, there is no wax or mud used by this bee. The leaf cylinder of the bee is half filled with a substance like condensed milk and on this the egg is laid.



Typical rock shelter in Seychelles showing massed pitchers of *Sceliphron* and *Eumenes*.

NOTES ON THE GENUS *ROPALIDIA* (HYMENOPTERA : VESPIDAE) FROM MADAGASCAR.

By D. VESEY-FITZGERALD, B.Sc., F.R.E.S.

INTRODUCTION.

THE following observations were made during the course of a short visit to Madagascar in the year 1939. The specimens collected were determined by Dr. J. Bequaert, of the Harvard Medical School, during 1940, to whom acknowledgment is made. Unfortunately most of the original notes made during the trip and a series of photographs illustrating nests and habitats were subsequently lost upon the Japanese occupation of Malaya.

However, since practically nothing appears to have been written about the nesting habits of *Ropalidia*, and since the collection included fifteen different species which is fairly representative of the known total from the island, it seems that it may be worth while to place on permanent record such notes as have survived.

Opportunities for collecting arose at Diego-Suarez, Nossi-Bé Island and adjacent mainland, Majunga, and thence at brief halts along the main road to Tananarive, at Perinet, a station on the railway in the east coast forest belt, and at Tamatave.

The majority of the specimens were taken in two rather distinct habitats, namely, coastal cultivations with largely secondary vegetation and inland primary forest; and the majority of the species were found in one or the other, but not in both types of environment.

Several of the forest *Ropalidia* exhibited the curious greenish coloration which is a character of many other genera of Madagascar Hymenoptera.

NOTES ON THE SPECIES.

Ropalidia anarchica de Saussure.

Comb leaf-shaped, supported by a single short stalk from the base of the initial cell, the remaining cells being built up along the sides of pre-existing cells. Cells 10 mm. deep tapering slightly towards the base of the cell from the mouth, which is 4 mm. across. Composed of very closely knit, rather tough, shiny material, which is laid down in bands of slightly varying colours.

The cells are sharply divided into two sizes. The larger are full-sized cells, containing pupae and larvae. These are the older cells towards the base of the comb. Towards the apex of the comb are a series of pocket-sized cells containing the egg and very young larvae. The larger cells have a glazed perforation in the base, but in the case of newer cells the base is entire. Vacated cells are cut down. Thus there is a zonation in cell-size. The base of the comb is composed of cut-down cells, which gradually increase in height to the full-sized cells in the central part of the comb and at the apex is an area of

pocket-like cells. The largest comb examined contained 340 cells and measured 9 cm. long and 3 cm. greatest width.

A single egg is laid in each cell. The pupal caps are convex at the mouth of the cell. When freshly spun they are pure white; later they become dirty coloured and they are ornamented on the outside with fragments of pulp. This species is a forest wasp, and it was collected upon three occasions at Perinet.

R. bicincta de Saussure.

An incipient comb containing three pocket-like cells, each with an egg, was being tended by a single female at the time of collection.

This species is a wasp of settled areas. A nest was found under the overhang of an earth bank at Ambanja, and another on the underside of a coconut leaf at Nossi-Bé.

R. carinata de Saussure.

A full-sized comb of this species was not found, but a lone female was found starting to build. The site chosen was amongst the foliage of a *Casuarina* tree at Majunga. Four pocket-like cells had been made, the first was fixed to the support by a stalk and the others were built onto the side of this first one. Although the cells were still so small and incomplete, three of them contained an egg.

R. dubia de Saussure.

The single nest of this forest-frequenting wasp which was found near Perinet was of particular interest. The site chosen was the lichen-covered trunk of a "travellers palm," *Ravenala madagascariensis*. The comb was a good-sized one, consisting of about 150 cells, and it was almost circular in shape. The whole was supported by a single broadened pillar, which subtended the first made cells at the uppermost point of the circumference. The interesting part about this comb was that it was set vertically, that is to say it lay parallel to the surface of the tree trunk, and the mouths of the cells, which lay in a horizontal plane, were pointing directly outwards.

The back of the comb was against the trunk, but there was sufficient space left for the wasps to pass between the comb and trunk.

Viewed from the front the comb strikingly resembled a more or less circular lichen patch on the trunk and as this resemblance was due to several separate factors, it is of interest to examine them in detail. In the first place the general circular shape of the nest created the general impression of a lichen patch. The material with which the comb was made was of a general brownish colour and rather tough. It was, however, freely mottled with splashes of green and white so that the whole harmonized very well with the other lichens on the trunk. The pupal caps were convex within the mouths of the cells. These were composed of opaque, rather dirty coloured silk, which made them inconspicuous; but more than this, they were freely splashed over with green fragments on the outside. Lastly, the adult wasps themselves, which spent their time resting on the surface of the comb, which was exposed to view, were extremely inconspicuous, since many of them were a suffused greenish colour.

The whole effect, therefore, was one of concealment by harmonizing with a natural lichen-covered background and the behaviour of the wasps was also in keeping with this general scheme. When disturbed, instead of flying to attack or even flying away, the wasps clung tenaciously to the comb and were quite difficult to drag off.

As usual, it was found that the new pocket-like cells, which were situated round the perimeter of the comb, had intact bottoms, while the full-sized cells, which measured 11 mm. deep by 4 mm. across the mouth, had a "glazed" window in the bottom. Vacated cells were being re-used, the egg being laid half-way down in one angle of the wall. The comb measured 65 mm. across the greater and 55 mm. across the lesser axis.

R. fraterna de Saussure.

This wasp was only collected on one occasion and that was on the island of Nossi-Bé. A little nest of nine incomplete cells had been placed on the underside of a coconut branch. The first cell was supported by a short stalk, the next two cells had been constructed on one side of this and the subsequent cells arranged in pairs, each pair at the side of the previous pair. The last three cells to be made had no perforation in the base. The rest of the cells, all of which contained larvae, were perforated and the perforation had been "glazed" over with a membrane. The first cell to be constructed was situated at the end of the supporting stalk, and therefore could not be perforated right at the top and so the glazed hole had been made rather to one side.

Although none of the cells were old enough to have produced a young wasp, three females were present on the nest. Each of these appeared to be co-operating in nest construction on an equal footing.

R. galimatia de Saussure (= *madecassa* de Saussure).

A single nest of this species was found in secondary forest at Perinet. It was situated on the underside of a wooden lichen-encrusted railing. The material composing the comb was laid on in mottled bands of greenish and brown colour, so that the nest toned into its surroundings remarkably well.

The comb was oval-shaped, 50 mm. by 35 mm., and supported by a single central stalk. There were ninety cells altogether; full-sized were 8 mm. deep and 4.5 mm. across the mouth. The newest cells were peripheral, pocket-like, unperforated and contained an egg each. The cells containing larvae had a very large "glazed" window in the top. The oldest cells in the centre of the comb had hatched out. These had been partially cut down and a new egg laid inside. Cells containing pupae were closed with a white, semi-opaque cap, which was freely splashed with nest material on the outside.

R. grandidieri de Saussure.

This species is one of the commonest of the genus in settled country. Specimens were collected at Perinet in clearings and areas of secondary growth; by the Kamoro river at Maevatanana; at Majunga and at Ambanja in the Sambirand. The common nest site was under the shelter of an overhanging earth bank, but combs were also found in the foliage of *Casuarina* trees. The comb is leaf-shaped—that is to say, the supporting pillar is at the narrowest

end of the comb, the cells being constructed in ever-increasing rows outwards on one side of this point. A new comb consisting of only three pocket-like cells, each containing an egg, was being attended by a lone female. The largest comb found measured 50 mm. long and 36 mm. greatest width and contained ninety cells. Full-sized cells, i.e. those containing pupae, were 9 mm. deep and 4 mm. across the mouth, but the egg is laid in a cell when it is only pocket-like and as the resulting larvae grows the cell is heightened. Old cells from which a young wasp has emerged are re-used and in this case the cell is usually, but not always, cut down in height. The roof of even the newly made cells is often perforated. At this stage it appears that the material of the roof is so thinly laid down that it has a threadbare appearance. Later a more definite perforation is made. An important detail is that the holes in the newest cells, which only contain an egg, are glazed over, so that it seems that this membrane must be placed there by the adult wasp and not by the larva, as might be the case in older cells.

Cells containing pupae are closed with a very convex cap of dirty coloured silk, which protrudes far beyond the mouth of the cell. This cap is ornamented with fragments of nest material.

R. hova var. *minor* de Saussure.

This species was very common in areas of secondary forest around Perinet. It goes in for gregarious nesting, which has not been observed in any other species. Should the selected site be the shelter of an overhanging earth bank, several combs, depending on the size of the place, will be hung in close proximity. But in certain more extensive and permanent sites, such as the underside of a concrete bridge, there may be many hundreds of combs closely packed together. Nest space may even become a limiting factor and in this case new combs have been seen hanging from old combs. These congregations are the scene of considerable activity, but it may be noted that no co-operation in the attack of an intruder is exhibited by the many families. Returning wasps, which appear to pitch on to their own comb without any hesitation, are welcomed by the other wasps already on the comb. The foragers bring in a ball, which is thought to be pulped caterpillars, and a sharing out of the load between all the wasps on the comb is usual. No other species of *Ropalidia* were ever found mixed in with these bands, but a *Sceliphron* female was seen busy building her mud cell in the midst of a thick throng of *R. hova*. The former came and went about her business quite unmolested. The wasps were, however, not so tolerant towards all their visitors. A parasitic fly was frequent about the combs and whenever adults of this species came near to a comb it was very definitely "warned off" by the wasps.

The individual combs were rather small. About 40 cells in a comb measuring 30 mm. by 25 mm. was the biggest. The combs were more or less circular or oblong and they were suspended from a short stalk situated at one side. A full-sized cell is 15 mm. deep and 5 mm. across the mouth. The full-sized cells, as in other species, had a glazed window in the top, and the new cells containing young brood were still short and had no perforation in the roof.

A very curious characteristic of this species is its habit of laying up to four eggs in each cell. More than one egg is the rule rather than an exception, but

the first larva to hatch crushes the other eggs or younger larvae, so that only one matures in each cell. The full-fed larva spins a dirty white opaque and convex cap across the mouth of the cell. When the young wasp has left the cell fresh eggs are laid within. Even cells which contain the empty puparia of a Dipterous parasite are laid in again, the egg sometimes being placed within the empty puparia. There is some evidence that this wasp sometimes lays in an old nest which she has not built, but conclusive proof of this fact is wanting.

Typical *R. hova* de Saussure was collected on several occasions in the forest at Perinet, where it was flying with a variety lacking thoracic markings, as well as with var. *minor*, which was the only form of which the nests were found.

R. ignobilis de Saussure.

Specimens were collected at Bas Sambirano (mainland opposite Nossi-Bé Island) on 19.ii.39, where this species was constructing nests under the overhang of an earth bank bordering a road passing through plantations of coffee and cocoa and patches of secondary-growth forest. Also occurs on Nossi Bé Island, but was not taken elsewhere in Madagascar.

R. pomicolor de Saussure.

Collected once in forest at Perinet on 4.ii.39.

R. schulthessi de Saussure.

This is a common lowland (coastal) species, which was collected at Ambanja and Majunga on the west coast and at Tamatave on the east coast.

It is a wasp of the humid cultivators, where its small combs are located on the underside of the broad (sheltering) leaves of coconuts, oil-palms and bananas.

Upon one occasion (Ambanja, 13.iii.39) a single female was found tending a comb of four pocket-cells each with an egg. On another nest (Tamatave, 17.iii.39) two females were found tending a comb of nine incomplete cells, each containing an egg. Although apparently no other brood had existed, two of the pocket-cells already had a glazed window in the base.

R. velutina de Saussure.

Collected upon a single occasion (2.ii.39) in the forest at Perinet. Nest not observed.

R. subclavata de Saussure.

Two specimens collected (2 and 4.ii.39) in the forest at Perinet. Nest not found.

R. phalansterica de Saussure.

This species was collected in the forest at Perinet (2.ii.39) as well as in a coconut plantation on Nossi-Bé Island (9.ii.39).

R. vitripennis de Saussure.

Collected once at Bas Sambirano (mainland opposite Nossi-Bé Island), on 19.ii.39.

SUMMARY.

Notes are given on the occurrence, habits and nest-construction of fifteen species of the genus *Ropalidia*.

BOOK NOTICES.

Principles of Animal Ecology. By W. C. ALLEE, ORLANDO PARK, ALFRED E. EMERSON, THOMAS PARK and KARL P. SCHMIDT. Roy. 8vo. Philadelphia and London (W. B. Saunders Co.), 1949. Pp. xii + 837, 362 figs. Price £3 10s.

In accordance with its title, this book aims at a study of the underlying principles of animal ecology, together with a summary of the evidence on which they are based. The text is divided into five sections: History of ecology, analysis of the environment, populations, the community, ecology and evolution.

The second section, that on analysis of the environment, includes a brief account of solar radiation as a source of energy, and the basic physics of heat, light, gravity, pressure and sound, in their impact on living organisms. We pass then to more complex environmental factors, including among others currents of air and water, the substratum, water, atmospheric gases, and soil.

Section III, on populations, and Section IV, on the community, deal with two different types of animal aggregation, and the effect upon them of environmental factors of the kind discussed in Section II.

Finally, Section V examines the effect of these ecological principles upon theories of evolution and consequently upon systematics.

There is an extensive bibliography and author-index, running to seventy-one pages, and a comprehensive subject-index.

How to Know the Immature Insects. By N. F. CHU. Pictured Key Nature Series. 8vo. Dubuque, Iowa (Wm. C. Brown Company), 1949. Pp. 234, 631 figs. Price \$2.00 (loose-leaf), or \$3.00 (cloth).

An illustrated key to the immature insects, compiled from such keys as exist in the different Orders. There are introductory chapters on the importance of immature insects, what they look like, where and how to collect them, and how to preserve and rear them.

Nearly every unit dealt with has at least one small illustration. There is a bibliography of important references, and a combined index and illustrated glossary.

THE EMBRYONIC RESPIRATION OF THE SHEEP BLOWFLY, *LUCILIA SERICATA* MG.

By R. C. RAINY, Ph.D., A.R.C.S., F.R.E.S.

(Department of Entomology, London School of Hygiene and Tropical Medicine.)*

MUCH of the information so far available on the embryonic metabolism of insects is due to the work of Bodine and his collaborators on the grasshopper *Melanoplus* during the last twenty years, and to that of a number of investigators, mainly towards the close of last century, on the silkworm *Bombyx*. Both these insects have a protracted egg stage, extending over a number of months and complicated by the occurrence of suspended development or diapause. The embryonic development of *Lucilia*, like that of many of the higher Diptera, is on the other hand extremely rapid, lasting only a matter of hours; and the embryonic metabolism of this species is of further interest in view of the specialized environment (carrion or living sheep) in which the eggs develop.

MATERIAL AND METHODS.

A stock culture of adult flies, originally established by the late Dr. W. M. Davies from sheep myiasis material collected in North Wales, was maintained in an insectary, heated during the winter months to maintain a temperature above the threshold of oviposition (18° C.—Hobson, 1935). Eggs were obtained by placing fresh lean beef in the cages for short periods, and subsequently maintained at 25° C.

A constant-pressure differential respirometer was used, of the type described by Dixon (1943, p. 7), but with cups similar to those used in Dickens' and Simer's first method (*ibid.*, p. 68), as modified by Herford (unpublished) for use with insect material. The apparatus consisted of two identical vessels connected to the opposite arms of a capillary U-tube containing Sudan III in kerosene; one arm of the U-tube was also connected to a 1 ml. graduated pipette into which measured volumes of mercury could be run from a screw-controlled reservoir. Each vessel was closed below by a special cup-shaped stopper in which the eggs were placed. When this stopper was in position, an annular trough in which reagents could be placed was formed around it; and in addition the vessel had a removable side-tube whose contents could be added to those of the trough during the course of the experiment without affecting the volume of the enclosed system. Both sides of the apparatus were provided with taps communicating with the outside air. The experiments were performed in a controlled-temperature room maintained at 23–25° C., with the apparatus immersed in an electrically stirred water-bath at 25° C., making it possible for the first readings to be taken within a few minutes of the introduction of the eggs into the apparatus.

For the continuous observations on oxygen uptake throughout embryonic development, saturated baryta was used as the absorbent, and a little M/250

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sulphuric acid was placed in the side-tubes to maintain a sufficiently humid atmosphere. With the small amounts of material used the rate of absorption of carbon dioxide was found to be adequate without continuous shaking. The respiratory quotients of batches of eggs at various stages were determined by Krebs' method (*ibid.*, p. 95). 0.15 ml. of 30 per cent. sodium iodide solution was added to a similar volume of M/250 sulphuric acid in each side-tube, and 2 ml. M/5 potassium permanganate containing M/500 sulphuric acid was placed in each annular trough. Volume changes representing the difference between oxygen uptake and carbon dioxide output were then followed for a suitable

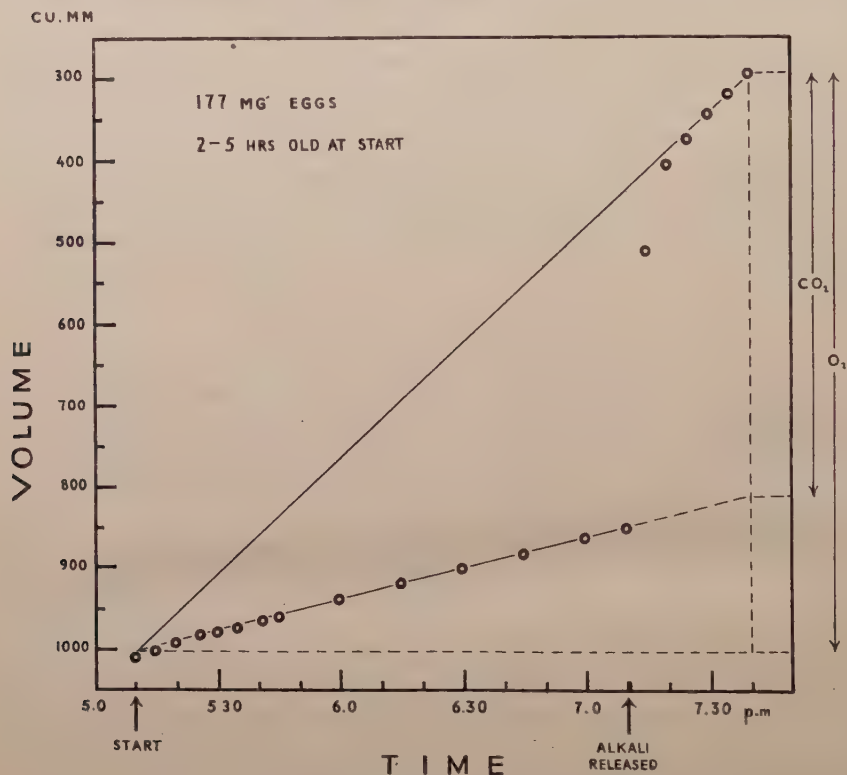


FIG. 1.—A typical respiratory quotient determination.

period. The reagents were finally mixed, producing a strongly alkaline solution, which with gentle shaking completely absorbed the accumulated carbon dioxide within 15–20 minutes. A typical set of observations is shown in fig. 1; the respiratory quotient was determined graphically in each case.

RESULTS AND DISCUSSION.

The rapid embryonic development of *Lucilia* made it possible to follow the oxygen uptake of duplicate batches of eggs continuously from shortly after oviposition until hatching (fig. 2). Each batch contained 200–300 eggs, laid over a period of half an hour, and any rapid changes in the respiratory rate

of the individual eggs are therefore likely to have been somewhat smoothed out in the results observed.

The agreement between the two batches was reasonably good, with the

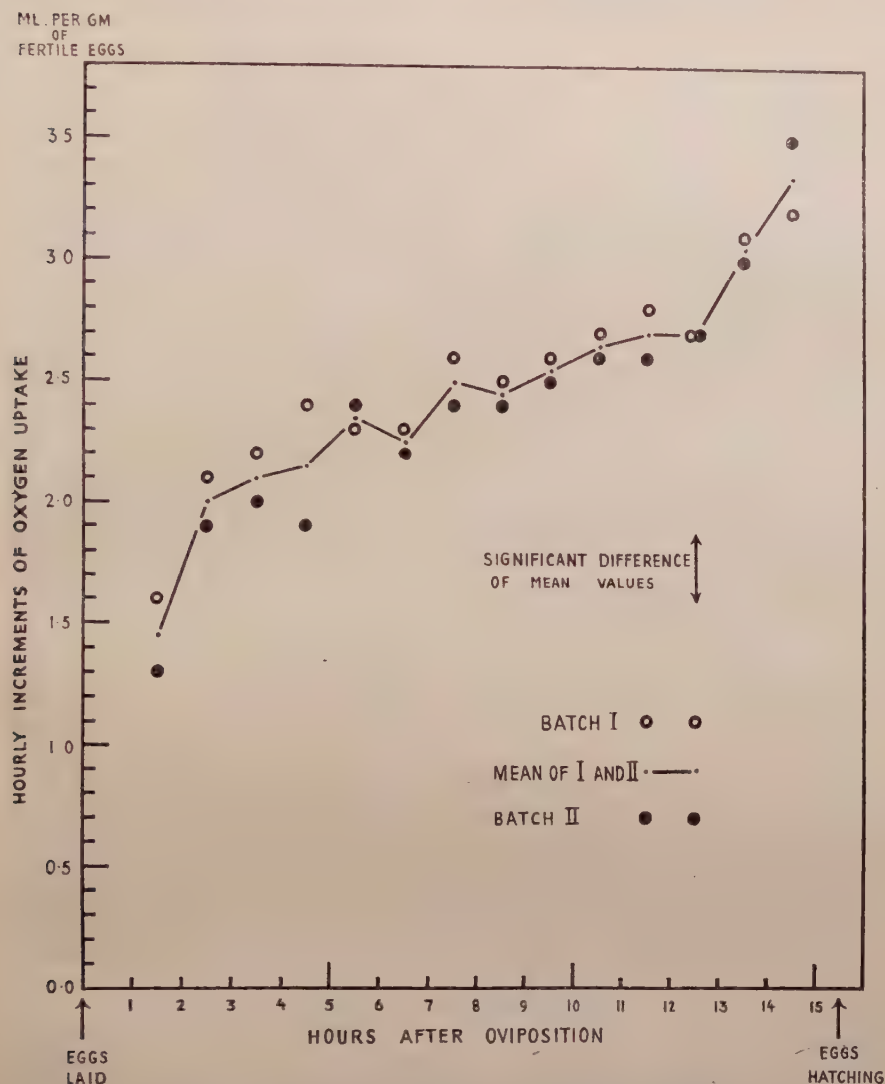


FIG. 2.—Oxygen uptake during embryonic development.

values from I averaging slightly (0.12 ml./gm./hr.), but significantly ($P < 0.05$) higher than the corresponding figures from II. This difference may perhaps represent some respiratory activity of the sterile eggs, of which batch I contained 4.2 mg. out of a total of 23.7 mg. eggs used, compared with 0.3 mg.

sterile eggs out of the 20.9 mg. of batch II. Fig. 2 also shows the difference between any two-hourly mean values required for significance at the conventional 5 per cent. level (0.28 ml./gm./hr.); the mean difference between batches has been eliminated as a "block effect" showing no consistent trend during development.

The respiratory rates observed—1.5 to 3.3 ml./gm./hr. at 25° C.—are very high compared with those previously recorded for insect eggs. In *Melanoplus*, for example, oxygen uptake at about 20° C. rises from 0.04 ml./gm./hr. in the newly laid egg to a maximum of 0.3 ml./gm./hr. at hatching (Bodine, 1929; Boell, 1935). Fink (1925), investigating the embryonic respiration of ten species of insects, mainly Coleoptera, recorded oxygen uptakes ranging from 0.0005 to 0.006 ml./gm./hr. at 21–24° C.; and Bodenheimer (1929) observed an oxygen consumption of 0.09 ml./gm./hr. by the eggs of *Schistocerca* at 24–25° C.

The moisture-content of the eggs is about 79 per cent., giving Q_{O_2} values of –6.5 to –14.4 c.mm. oxygen at N.T.P. per hour per mg. dry weight. These values, determined at 25° C., are of the same order as those found for mammalian tissues at considerably higher temperatures; Dixon (1943) quotes values of Q_{O_2} at 37° C. ranging from –3.2 for dog pancreas to –30.7 for rat retina.

This association of high respiratory rate with rapid embryonic development invites comparison with the corresponding data for the chick and silkworm, for which a considerable measure of agreement in total energy loss during the complete development of unit weight of egg has been demonstrated (Needham, 1931). The total oxygen uptake during the complete development of 1 gm. of *Lucilia* eggs was 36 ml. at 25° C., which, assuming a calorific quotient of 3.3 gram-calories per mg. oxygen, corresponds to the liberation of 160 gm. cals. If embryonic respiration may be assumed to account for the whole of the energy lost during egg development, as it does in the chick, then this figure of 160 gm. cals. provides a measure of the energy loss during the complete development of one gram of *Lucilia* eggs—Tangl's *Relative Entwicklungsarbeit*. The corresponding figures for the chick and silkworm, respectively 810 and 880 gm. cals., are substantially higher than that for *Lucilia*. This suggests that these quantities depend to some extent on the duration of development; in the silkworm embryonic development extends over a week before hibernation and about a fortnight after it, so that the period of active metabolism is similar to that of the chick, and about thirty times longer than that of *Lucilia*.

The production of 160 gm. cals. during the 15 hours of embryonic development of 1 gm. of *Lucilia* eggs at 25° C. corresponds to an average metabolic rate of 250 Cal./kg./day. The metabolic rate of the chick at hatching is about 100 cal./kg./day—at a temperature 12° higher; and the highest figure cited by Needham (1942), in discussing changes in basal metabolism during the life-history of a considerable range of mammals, is only 210 cal./kg./day (for month-old rats).

The recorded increase in respiratory rate, from 1.5 ml./gm./hour soon after laying to 3.3 ml./gm./hour just before hatching, no doubt reflects as in other animals the progressive increase in the relative proportion of respiring embryonic protoplasm at the expense of inert reserve materials.

The respiratory quotient results are summarized in Table I.

TABLE I.—*Respiratory Quotients during Embryonic Development.*

Age of eggs at start of determination (hours).					Respiratory quotient.
$\frac{1}{2}$ – $1\frac{1}{2}$	0.64
1–2	0.72
2–5	0.73
4–7	0.73
8–9	0.75
9– $10\frac{1}{2}$	0.76

The values observed, ranging from 0.64 to 0.76, suggest that the main substance catabolized is fat, and, while some of the complications of interpreting the R.Q. values found during insect development have been indicated by Hill (1945), this conclusion is supported by the corresponding analytical data. Thus Needham (1942), using observations already recorded on the composition of the egg and larva of *Lucilia* (Rainey, 1938), together with determinations by Brown (1938) of the nitrogenous end-products accumulating during embryonic development, has estimated that fat and protein contribute respectively >95 per cent. and <5 per cent. of the total material catabolized during embryonic development. In three other terrestrial animals (*Melanoplus*, *Bombyx* and *Gallus*) fat similarly accounted for 64–91 per cent. of embryonic catabolism, while in nine aquatic animals protein provided 37–90 per cent. of the material so combusted. Needham further estimated from the same data that only 0.5 per cent. of the protein initially present in the *Lucilia* egg is combusted as a source of energy during embryonic development. Other terrestrial eggs (silkworm and chick) gave corresponding figures of less than 5 per cent., while nine aquatic animals gave values ranging from 14 to 41 per cent.

One gm. of *Lucilia* eggs loses some 14–22 mg. of fatty acids during embryonic development (Rainey, 1938); and 1 mg. of oleic acid, a representative fatty acid, requires for complete combustion 2.2 ml. of oxygen at 25° C. The recorded loss of fat would therefore require for its oxidation some 31–48 ml. of oxygen, as compared with the total observed oxygen uptake of 36 ml. Within the limits of accuracy of these data, fat catabolism is thus capable of accounting for the whole of the oxygen uptake during embryonic development.

Despite the almost aquatic nature of the environment into which the *Lucilia* egg is often laid, and its inability to resist desiccation, the embryonic metabolism is thus of the usual cleidoic terrestrial type, in which the predominantly protein catabolism of the primitive aquatic egg has been largely replaced by a catabolism of fat, which can be oxidized completely to carbon dioxide and water without the difficulties involved in the disposal of nitrogenous end-products from a closed system.

Needham has also suggested (1931) that the ontogenetic succession of energy-sources (carbohydrate-protein-fat) found in the developing chick, and reflected by changes in its respiratory quotient, might be of general occurrence. Boell (1935) reported an initial R.Q. of 0.95 in *Melanoplus* eggs, falling rapidly to an average of 0.71 throughout later embryonic development, and corresponding analytical data on fatty acids (Slifer, 1930) and carbohydrates (Hill, 1945)

provide further evidence of such a succession in this species. Similar results have also since been recorded for the eggs of a fish, a crab, and gephyrean and nematode worms (Needham, 1942). The present results do not show an initially high R.Q., though the carbohydrate-protein stages might perhaps have been passed through prior to the first R.Q. determination.

SUMMARY.

(1) Oxygen-uptake has been recorded throughout embryonic development in *Lucilia*, and determinations of the respiratory quotient have been made at intervals during this period.

(2) The respiratory rate is very high compared with that of other insect eggs with a longer period of development, and is of the same order as that given by mammalian tissues at a considerably higher temperature,

(3) Respiratory quotients of 0.64–0.76 suggest fats as the chief energy source, a conclusion supported by corresponding analytical data.

ACKNOWLEDGMENTS.

This work was carried out during the tenure of a pre-war Agricultural Research Scholarship; I am greatly indebted to Professor P. A. Buxton and Dr. V. B. Wigglesworth for their active interest in it, and to Dr. D. L. Gunn for assistance with recent literature.

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FIELD NOTES ON THE MATING HABITS OF *SARCOPHAGA* MEIGEN (DIPTERA).

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FROM a field study of Oriental species of *Sarcophaga* in the region of Chungking (Koloshan), Szechuan, China, it is clear that the adults of certain species show food preferences. Thus, for example, *S. knabi* Parker, *S. fuscicauda* Böttcher and *S. albiceps* Meigen are to be found on human faeces; *S. caudagalli* Böttcher and *S. brevicornis* Ho have only been found on dead snails (*Viviparus chinensis* Gray) by the edges of ponds; *S. besoni* Senior-White and *S. tsushimae* Senior-White have only been found sucking the sap from wounds on certain trees (*Quercus serrata* Thunb.). While other species also frequent particular localities their distribution has not yet been correlated with particular food preferences, and as far as is known they are not faeces-feeders. *S. erecta* Ho occurred exclusively on the rocks of mountain streams; *S. josephi* Böttcher was found in the vicinity of hot springs; *S. orientaloidea* Senior-White was confined to the tops of sandy hillocks; and *S. melanura* Meigen was generally taken on vegetation. So constant were these habits that one could be almost certain of collecting a given species in the locality indicated here, and, except for the most common species (*S. fuscicauda*, *S. knabi*, *S. albiceps*), one would not expect to find any of the above species visiting a locality other than that named as characteristic.

These observations were made in a small area of about four square miles of hilly country; the hot spring locality is not, however, included in this area. It seems possible that certain environmental factors, among which the food factor may be important, result in the limitation of a particular species to a particular restricted environment and so facilitate the meeting of the sexes and augment the chances of mating.

The mating habits of coprophagous *Sarcophaga* may be conveniently studied in the field on human faeces. Within a very short time of deposition, *Sarcophaga*, *Chrysomya*, *Lucilia* and other faeces-frequenting flies assemble and begin to feed. At the height of summer, the first fly may arrive within a minute of deposition.

In these faeces-feeding species, copulation usually takes place after feeding when both sexes, but especially the female, are gorged. The male takes the initiative and may attempt to copulate with a number of flies in succession; it mounts, vibrates the wings violently, and endeavours to hook the terminalia under the hind end of the other fly. Copulation is attempted by the male irrespective of genus, species or sex. Thus it may visit a *Lucilia*, a male *Sarcophaga*, a female *Sarcophaga* (but of a different species), and so on, until a female of the same species is found. Indeed, the correct selection of the female by the male may take some time, and it seems that the "right" mate is found by trial and error; the female apparently provides no specific behaviour or chemical stimulus which can serve for recognition by the male.

This momentary pairing of flies of different species may deceive the collector interested in catching the sexes *in copula*. Though a pair of *Sarcophaga* may

fly away together, apparently interlocked, it does not necessarily follow that penetration has taken place (or, conceivably, if penetration has taken place, that the genital organs of the male and female are "compatible"). It is inadvisable, therefore, to assume conspecificity of specimens which have just paired off. Only pairs that have really settled down together should be presumed conspecific.

The initial stages of copulation are usually interrupted by violent wing-movements on the part of the female. The pair may remain where the female was found (i.e. on the faeces), or may fly away to some nearby shrub. Pairs on the faeces may lose their balance and tumble to the ground.

Even when the pair is not in flight, either or both partners vibrate the wings from time to time, producing a characteristic sound—very much like that made by a fly confined in the folds of the collecting net. This sound is usually the first indication that a mated pair is close at hand.

A copulating pair may fly from shrub to shrub or for many yards if disturbed. Undisturbed, they usually do not fly about. When approaching a feeding site, it is a good policy to examine first the bushes in the surrounding area for copulating pairs and then to work carefully inwards towards the site in a circular fashion; pairs may be disturbed if the collector walks directly to the centre of activity.

Sarcophaga copulate for considerable lengths of time; a mating pair has been watched for four consecutive hours. The species was a faeces-feeder, probably *S. knabi* Parker.

Copulation takes place at any time of the day, but pairs are most abundant in the heat of the day. Twilight and on-coming rain seem to induce mating pairs to separate.

The phallosome of the male may show rhythmical forward and backward movements during copulation, or may remain stationary in the female genital canal.

The separation of the sexes may be quite peaceful; the male withdraws its genitalia while still on top of the female and then flies off, leaving the female. Alternatively, the female may suddenly throw off the male with much stamping of feet and beating of wings.

Sometimes a male is to be seen attempting to copulate with an already copulating pair. The copulating male seems quite undisturbed in this case, there is no violent fluttering of the wings.

Sarcophaga taken in the field have not been observed to copulate in close captivity. In one case (*S. gigas* Thomas), however, a pair was seen to copulate soon after emergence and before feeding.

Position Adopted by *Sarcophaga* During Copulation.

The attitude assumed is the median ventral position (Richards, 1927); the male is above and both face in the same direction (fig. 1). There is no change of position during copulation.

If the male and female are of about the same size the claws of the fore legs of the male are usually hooked on to the base of the wing of the female (fig. 1); if the male is much larger than the female, the fore legs of the male rest on the head of the female; if the male is much smaller than the female, the fore legs of the male grasp on to the abdomen of the female.

One usually finds, however, that mating partners are of similar size. If the couple is resting on a smooth, flat surface, the middle legs of the male are generally close to the female abdomen with the feet not quite on the ground; they are also lateral to the middle legs of the female. The hind legs of the male rest on the surface behind the female. The fore and middle legs of the female rest on the substratum; the hind legs may periodically stroke the flanks of the male abdomen (the 4th and 5th abdominal segments); if no stroking occurs, the legs rest on the ground. During the stroking movement, the hind legs of the female are lateral to the middle legs of the male and medial to the hind legs of the male (fig. 1).



FIG. 1.—Diagram of *Sarcophaga*, in copula. The male (black legs) is above the female.

If the couple is resting on an irregular or inclined surface, all the legs of both the male and female, except the fore legs of the male, rest on the ground.

The male terminalia are protracted and hook round the female terminalia from above, pulling back the female terminalia. These constitute a larvipositor; they are not telescopic, but more or less flush with the end of the abdomen. The 5th sternite of the male—a V-shaped sclerite beset with bristles—sits like a saddle on the 5th or 6th tergite of the female. Most of the under surface of the male abdomen is not in close contact with the back of the female abdomen.

It follows from the median ventral position adopted by the copulating flies that:

(1) Only the female can walk. This it does as it is feeding; or if it is on a shrub it may alter its position to find a better hiding place; thus if a pair on a leaf facing the collector is approached, the female may walk to the other side of the leaf.

(2) Only the female can continue feeding. On the faeces one often sees several mating pairs with the females feeding and apparently behaving as if the males were not there.

(3) Only the male is free to defecate. The male, in fact, does so during copulation. The anus of the female, however, is blocked by the genital atrium of the male (fig. 2), and it is only after the pair have disengaged themselves that the female can defecate.

When the copulating pair is in flight it is the female that flies—the male is carried. This is not so when the female is much smaller than the male. Thus,

in the case of a large male and a very small female of *S. orientalooides*, the male was seen to use its wings. A copulating male is usually unresponsive to external stimuli; thus one can tickle the back of a mating male with a blade of grass, or, indeed, stroke it with one's finger, without the male paying the slightest attention. If, however, one applies the same treatment to the female, it immediately flies away with the male. It appears, therefore, that during copulation the female remains normally responsive, at least as far as the flight-reflex is concerned; *the female* is on the alert. For instance, if we approach too closely to the couple resting on the leaf, the female stops fidgetting at once and crouches motionless in a characteristic attitude, ready to spring off into flight at any moment.

A Closer Study of the Relations of the Genital Parts During Copulation.

For this study, the male and female were caught *in copula* and killed without being separated. The abdomens were snipped away from the bodies, macerated and dissected.

This account describes the relations of the male and female genital parts when the claspers, phallosome and forceps of the male actually enter the genital canal (the vagina) of the female (fig. 2). This is the only method of copulation in *Sarcophaga* known to the author (see, however, Patton and Ho, 1938). Patton's terminology (1934) is used for the various parts of the terminalia.

The forceps (paired) are found against the ventral wall of the female canal, and the claspers (two pairs—anterior and posterior) against the dorsal wall; with the claspers above, the forceps evidently dilate the female canal dorso-ventrally. The phallosome lies between the prongs of the forceps well in the female canal; the surface which carries all the projections (the true ventral surface) is applied to the dorsal wall of the female canal, and the smooth opposite surface (the true dorsal surface) is applied to the ventral wall of the female canal.

In the living male it can be shown that the anterior claspers move antero-posteriorly in the long axis of the body and the posterior claspers move in a lateral direction. When the specimen is pinned down suitably and its terminalia extracted, the posterior claspers may be seen to swing out laterally; this is followed by the anterior claspers swinging backwards and coming to lie medial to the posterior claspers. In copulation, one of the main actions of the posterior claspers is evidently to dilate the female canal from side to side, and an important action of the anterior claspers is to pull back the canal. The claspers are generally hooked and sharply pointed and probably dig into the soft dorsal wall of the female canal, providing a firm hold for the claspers to exert their actions. In many species the dorsal wall of the female canal is sclerotized; it is not a segmental sclerite, however. This sclerotization may be important in preventing the sharp-pointed claspers penetrating the wall of the canal.

In *Sarcophaga* the accessory plates of the male are apparently functionless in copulation; they are small and hardly enter the female canal. This is probably by no means so in the case of its homologue (G. C. Crampton calls them *surstyli*) in other genera, e.g. *Calliphora*, *Lucilia*, etc. Whether the

accessory plates are functional or non-functional is probably related to the development (Thomas, in press) of the bacilliform sclerites (Crampton) in the various genera. In *Sarcophaga* these are reduced to minute sclerites.

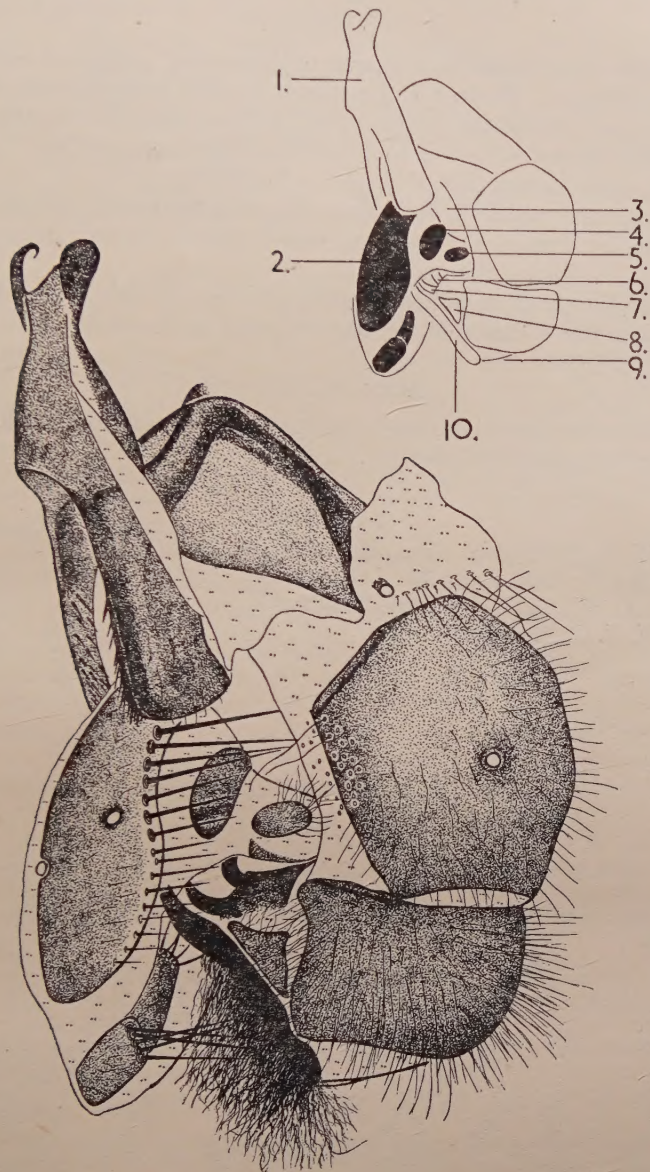


FIG. 2.—A dissection of the male and female terminalia of *Sarcophaga*, in copula, showing the relations of the various parts. The terminalia are slightly separated from each other. Inset: Sclerites of the female terminalia are in solid black. 1, Sternite 5 (male); 2, tergite 6 (female); 3, genital atrium (male); 4, ? tergite 9 (female); 5, anal cerci and anus (female); 6 anterior claspers (male); 7, posterior claspers (male); 8, accessory plate (male); 9, anus (male); 10, forceps (male).

The 5th sternite of the male seems to act as a vice, gripping the tip of the female abdomen during copulation and so allowing the forceps and claspers to perform their respective functions.

SUMMARY.

This paper describes certain aspects of the mating behaviour of the flesh-fly, *Sarcophaga* Meigen. Several of the species studied seem to have definite food preferences and among the faeces-feeders at least, this is evidently one of the factors which draws a species to a particular environment and increases the opportunities of the meeting of the sexes for mating.

In the vicinity of the food (faeces) the male apparently selects the female of its species by a process of trial and error ; the female does not seem to exert a specific attraction on the male.

A description is given of the position adopted by *Sarcophaga* during copulation, and of the relations of the various parts of the genitalia *in copula*.

ACKNOWLEDGMENT.

The author wishes to acknowledge his indebtedness to Dr. W. H. Thorpe for reading through the manuscript.

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